

The Proboscidian System in Nemertines.

By

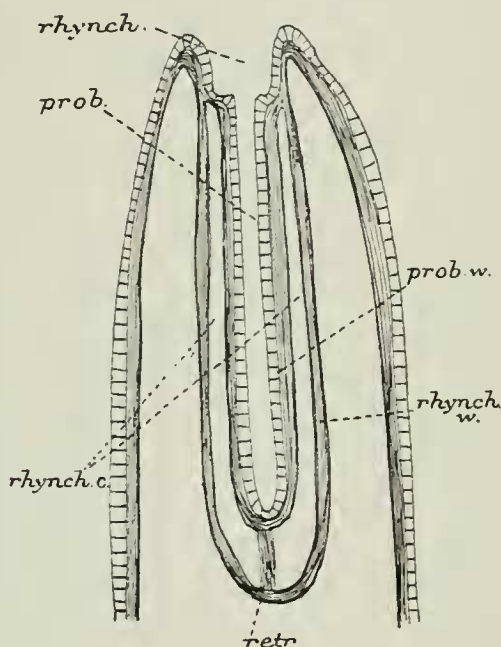
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With 36 Text-figures.

THE proboscis, together with its sheath and the rhynchodæum, are among the most characteristic features in the anatomy of Nemertines, so characteristic even that the system is not absent in any known species, neither of Anopla nor of Enopla. And wherever it is found, the whole system shows the same advanced development of construction; all three organs are completely developed, the proboscis being an introvertible tube, which is fastened to the body-wall at the anterior end of the rhynchocœl, and is connected posteriorly by a retractor muscle to the wall of the sheath. The rhynchodæum is a kind of atrium to the apparatus, through which the proboscis is everted (Text-fig. 1). Both proboscis sheath and proboscis itself possess a muscular wall, and the lumen of the sheath is lined by an endothelium. The cavity of both rhynchodæum and proboscis is lined by continuous epithelium that shows a differentiation of glandular elements in different parts of the system. The proboscis, therefore, consists of three layers—an epithelium, a muscular coat and an endothelial layer; the wall of its sheath of two—an endothelium and a muscular coat. The whole system is imbedded in the body-parenchyma. It has for a long time been assumed that the proboscis had developed out of a retractile part

of the head independently of corresponding structures in other invertebrates. Hubrecht (16) shared this opinion, and tried to explain, by the histological facts shown by the "Challenger" material, that the sheath had developed out of muscular elements in loco, and was an independent structure. However, Salensky (25) had published another hypothesis, comparing the whole proboscidean system of

TEXT-FIG. 1.

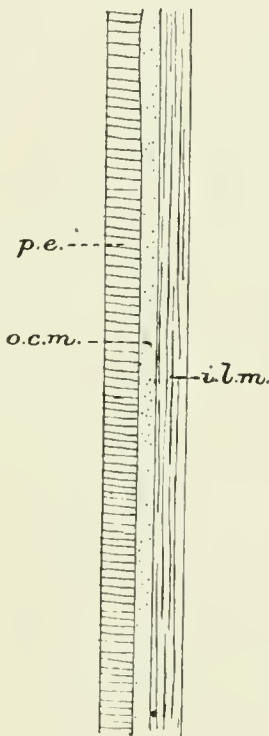


Schema of the proboscidean system in Nemerteans after Salensky (26). *rhynch.* Rhynchodæum or proboscis introvert cavity. *rhynch. c.* Rhyncho-cœlomic cavity. *prob.* Epithelium of the introverted proboscis. *prob. w.* Proboscis wall. *rhynch. w.* Wall of the proboscis cavity (rhynchocœl). *retr.* Retractor muscle of the proboscis. Compare with Text-fig. 36.

Nemerteans with the proboscis of the Rhabdocœlida proboscida. He founded his theory on certain embryological facts denied by Hubrecht (15), who tried to find support for his view in anatomical facts. Bürger (8) looked for a homologue of the whole system in the pharynx and pharyngeal sac of the Polyclads, but neither Bürger nor Hubrecht could gain the agreement of Salensky, who published

two articles in 1909 (27) and 1912 (28) in which he maintains his views of 1884 (25). As Salensky only gives embryological facts, we shall have to look for further judgment to the anatomical data. Wishing to draw my own conclusions as to the value of Salensky's theory, I have compared whatever was known about rhynchodæum, proboscis and proboscis sheath in Nemerteans.

TEXT-FIG. 2.

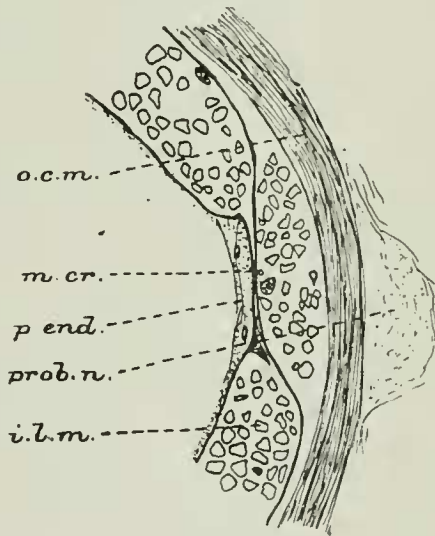


Schema of the proboscis of Palæonemerteans. *p.e.* Proboscis epithelium. *o.c.m.* Outer circular musculature. *i.l.m.* Inner longitudinal musculature.

The first fact that came to light was the great difference in structure between the proboscis of armed and unarmed Nemerteans. For the difference between the two does not consist only in the presence or absence of the so-called stylet; it is shown also in the structure of the muscular coat, and in the differentiation of the tube into different parts. It is even possible in *Enopla* that the armature has got lost, as seems to be the case with the genus *Planktonemertes* (10A). Mala-

cobdella also does not possess an armed proboscis. The Anopla show a great variety of structure for such a plainly built organ. The tube always consists of two parts, the anterior part sometimes possessing a differentiated region near the insertion to the body-wall. That a difference of epithelial glands exists between these parts is nearly certain; the exact nature of this difference, however, is not sufficiently known. Very often the beginning of the hinder part is

TEXT-FIG. 3.



Section of the proboscis of *Carinoma* after Bergendal (6, text-fig. 55). *prob.n.* Proboscidian nerve. *p.end.* Proboscidian endothelium. *o.c.m.* Outer circular musculature. *i.l.m.* Inner longitudinal musculature. *m.cr.* Muscle crosses.

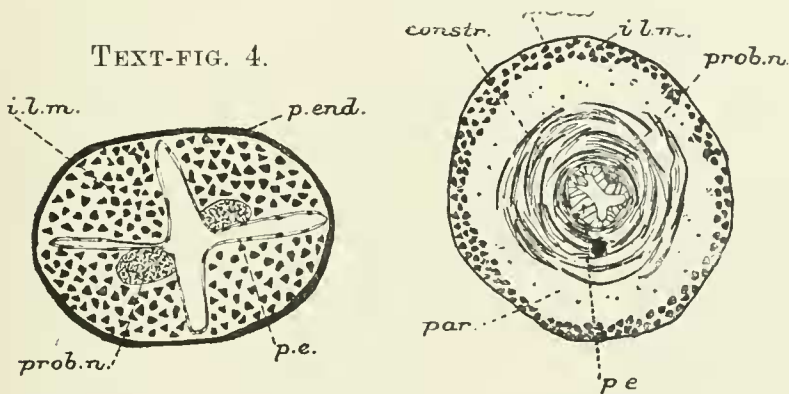
marked by a constriction. The principal seat of the variety of structure, however, is the muscular wall of the proboscis. In all Palæonemerteans the muscular sheath of the proboscis consists of two layers, a circular and a longitudinal, of which the circular layer is situated directly beneath the epithelium (Text-fig. 2).

Exactly this type of proboscis is found in several species of *Tubulanus* (9), in *Procarinina atavia* (5), in *Carinina* (9), *Hubrechtia* (9) and *Hubrechtella* (3). The other genera possess a more complicated proboscis, though, along the

greater part of each, the two muscular layers described above are developed. Moreover, Bergendal described in *Carinoma* (6) a proboscis in which the circular muscle-fibres show a tendency to divert into the longitudinal layer and build muscular crosses (Text-fig. 3). A circular layer outside the longitudinal fibres is, however, not present. As the tendency to form crosses is also known in the circular fibres of the body-wall, their presence in the proboscis of *Carinoma* cannot alter our opinion that only two muscular coats are present.

The genera *Cephalothrix* (33), *Cephalotrichella* (33) and

TEXT-FIG. 5.



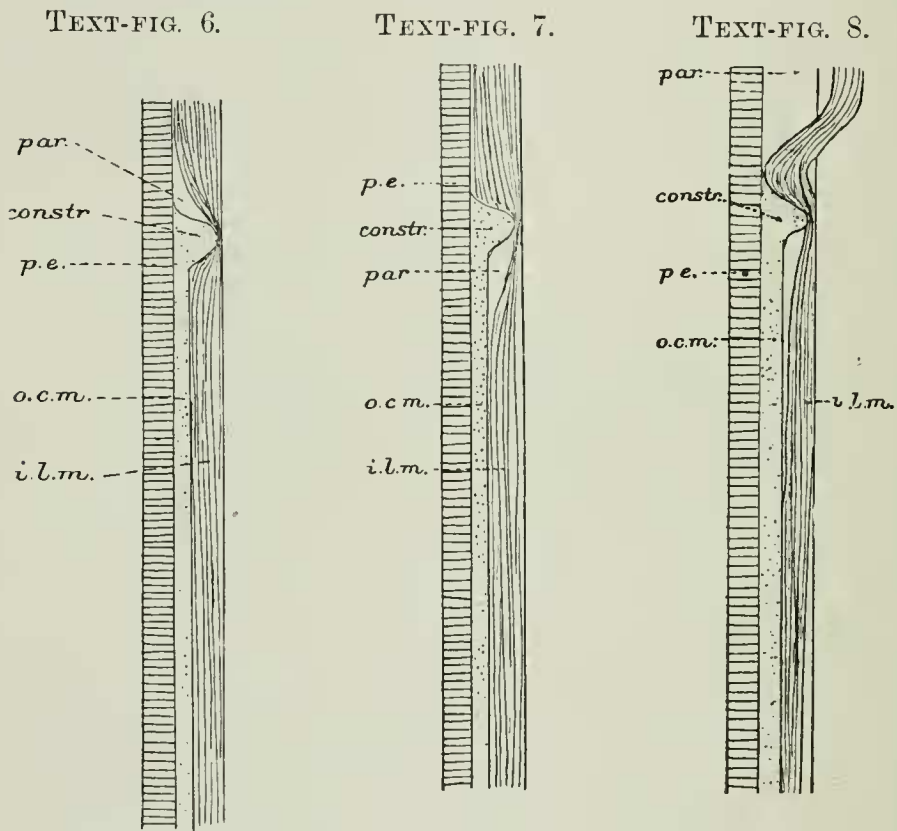
TEXT-FIG. 4.

TEXT-FIG. 4.—Proboscidian section of *Carinesta anglica*, Wÿnhoff. *p.e.* Proboscis epithelium. *i.l.m.*, *prob.n.* and *p.end.* as in Text-fig. 3.

TEXT-FIG. 5.—Proboscidian section of *Carinesta orientalis*, Punnett. *p.e.*, *prob.n.*, *p.end.* and *i.l.m.* as before. *par.* Parenchyma. *constr.*, Constrictor muscle.

Procephalothrix (33), *Callinera* (2), *Carinesta* and *Carinomella* (12) differ more from the above-mentioned type. In all of them the circular muscle-fibres are wanting in the portion directly behind the insertion of the proboscis (Text-fig. 4). In the family *Cephalotrichidae*, as well as in the three other genera, this part is followed by a conspicuous thickening of the circular layer, which acts as a constrictor (Text-fig. 5). At different places in this neighbourhood, in *Cephalotrichidae* just before (Text-fig. 6), in *Callinera* behind (Text-fig. 7), in *Carinomella* (Text-fig. 8) before and behind the constrictor muscle, the parenchyma is particularly well developed, causing a regres-

sion of the muscular fibres. The longitudinal fibres, however, are present over the whole length of the proboscis (Text-figs. 6 and 7), though often much reduced, as at the places mentioned above. In *Carinomella* (Text-fig. 8), however, the whole circular musculature has degenerated in the anterior part of the proboscis, and instead of four bundles of muscle-



TEXT-FIG. 6.—Schema of the proboscis of *Cephalothrix*. *pe.*, *par.*, *o.c.m.*, *i.l.m.*, and *constr.* as in Text-figs. 3 and 5.

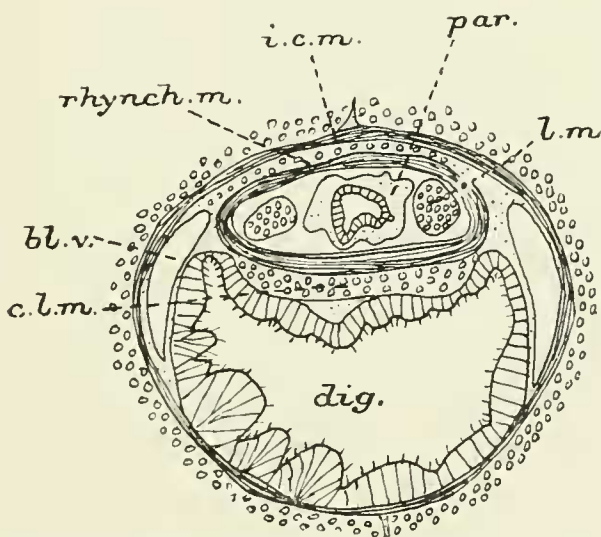
TEXT-FIG. 7.—Schema of the proboscis of *Callinera*. Letters as in Text-fig. 6.

TEXT-FIG. 8.—Schema of the proboscis of *Carinomella*. Letters as in Text-fig. 6.

fibres, as in *Cephalotrichidæ* and *Callineridæ* (*Carinesta* [Text-fig. 4] and *Callinera*), Coe (12) found only two longitudinal muscles in the cavity of the sheath, connecting the wall of the sheath with the anterior part of the proboscis (Text-fig. 9). The other parts of the proboscis, however, consist, in all these genera, of the same layers as in *Tubulanus* (Text-fig. 2); it

seems, therefore, not too presumptuous to say that in all Palæonemertines the muscular coat of the proboscis is composed of two layers, a circular and a longitudinal, the latter being situated beneath the endothelial surface. The deviations from this type, found in the families of Cephalotrichidæ, Callineridæ, and the genus *Carinomella*, have merely been brought about by the disappearance of the circular fibres in the region directly behind the insertion, accompanied in *Carinomella* by the egression of the longitudinal fibres.

TEXT-FIG. 9.

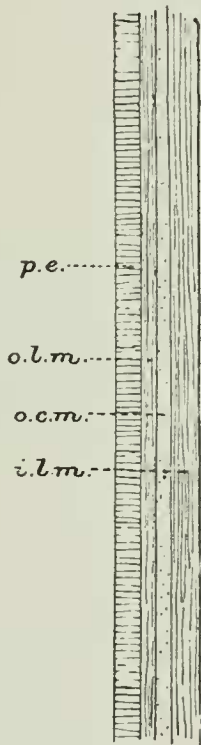


Section through *Carinomella* after Coe (12), fig. 54. *l.m.* Longitudinal muscle. *rhynch.m.* Rhynchodæal musculature. *c.l.m.*, Central long musculature. *i.c.m.* Inner circular musculature. *bl.v.* Blood-vessel. *dig.* Digestive tract. *par.* Parenchyma.

In Heteronemertea the proboscis shows a much greater variety of structure. A certain number of species possess a proboscis exactly like the Palæonemertea; the outer layer of the ejaculated duct consists of the glandular epithelium, next to it is the circular muscle-layer, limited at the other side by the longitudinal fibres; such are the proboscides in *Micrella rufa*, Punnett (22), *Oxypolia beaumontiana* Punnett (22), and in *Euborlasia* (9). The genera *Lineus*, *Cerebratulus* and *Micrura*, which are so closely connected, that they cannot even be distinguished from each other by anatomical features

alone, show a marked resemblance in their proboscides too. In all three genera species are known with two muscular layers, others possessing a third muscular coat (Tex-figs. 10 and 11). Representative of the Palæo-type are *Cerebratulus urticans* (J. Müll.) (9), and *C. greenlandicus* Punnett (23), *Lineus scandinaviensis* Punnett (24), and *L.*

TEXT-FIG. 10.



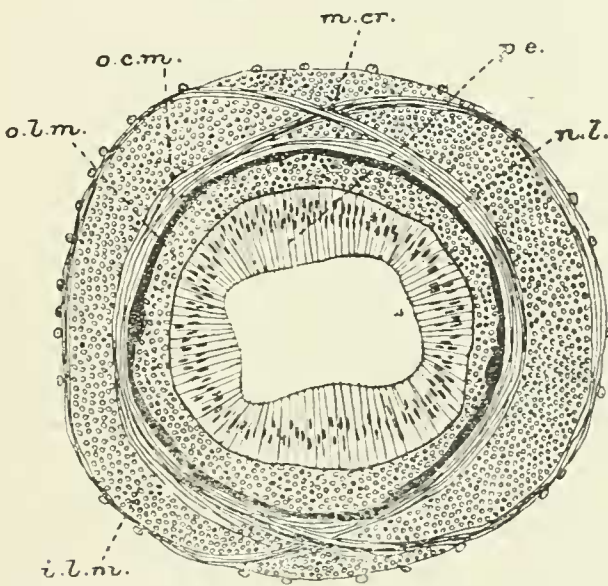
Schema of the proboscis of Heteronemerteans (*Cerebratulus marginatus*). *o.l.m.* Outer longitudinal musculature. *p.e.* Proboscis epithelium. *o.c.m.* Outer circular muscular layer. *i.l.m.* Inner longitudinal muscular layer.

bilineatus McIntosh (9), *Micrura varicolor* Punnett (24), *M. bergenicola* Punnett (24), and *M. atra* Punnett (24). Variations on this scheme are found in Heteronemerteans as in Palæonemertines. Miss Thompson (30) described the interesting genus *Zygeupolia*. The circular muscle-layer fails in the region behind the insertion, exactly as in *Cephalotrichidæ* and *Callineridæ* (Text-fig. 12). Other genera and species possess three muscular layers in the proboscis; to this

group belong the *Cerebratulus*-, *Lineus*-, and *Micrura*-species as *Cerebratulus marginatus* Ren. (9), and *C. eisigi* Bürger (9), *Micrura fasciolata* Ehrenberg (9), and *Lineus versicolor* Bürger (9). Two of these three layers consist of longitudinal fibres and they are separated by the circular muscle-fibres (Text-fig. 10).

The presence of this third layer in the proboscis of Hetero-

TEXT-FIG. 11.



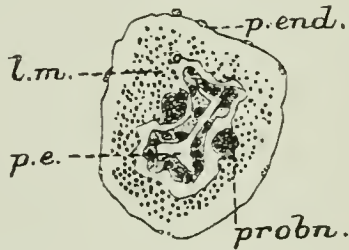
Section of the proboscis of the introverted *Cerebratulus marginatus* after Bürger (9, taf. 23, fig. 1). *m. cr.* Muscle crosses. *o. c. m.* Outer circular muscular layer. *o. l. m.* Outer longitudinal muscular layer. *i. l. m.* Inner ditto. *n. l.* Nerve layer. *p. l.* Epithelium (outer surface) of the proboscis.

nemerteans is rather striking. The acquisition of a longitudinal muscle-layer between the epidermis and the circular muscle-layer is characteristic of the body-wall in this group of Nemertines. The new layer in the proboscis wall, therefore, being also a longitudinal layer, can immediately be compared with the outer longitudinal layer of the body-wall, and, as its surroundings are exactly the same, it is laid down as part of the outer longitudinal muscle-layer. The circular coat of the proboscis in that case must be the outer circular muscle-layer of the body-wall, and the original longitudinal

layer is part of the inner longitudinal layer of the body-wall. The Palæotype of proboscides consists of the epithelium, the outer circular and inner longitudinal muscle-layers, that also form part of the body-wall. The newly obtained layer of the Heteronemertans has not yet been acquired by all proboscides; those with the Palæotype have not got it at all, the genus *Parapolia* Coe (11), is in the act of acquiring it (Text-fig. 13). In the hinder part this proboscis shows the Palæotype, in the anterior part the Heterotype.

A peculiarity of the circular muscle-layer of Heteronemertine-proboscides is shown in fig. 11. Some circular

TEXT-FIG. 12.



Section of the proboscis of *Zygeupolia* after C. B. Thompson (30).

p. end. Proboscis endothelium. *l. m.* Longitudinal muscles.

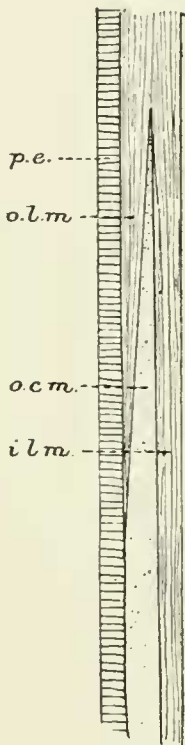
p. e. Proboscis epithelium. *probn.* Proboscis nerve.

fibres are seen to divert from their original stratum and to form crosses by entering the inner longitudinal coat, as I shall henceforth call it, conformable to the corresponding layer of the body-wall. These fibres of the muscular crosses continue even outside the longitudinal layer, constituting something like a very thin and very incomplete circular layer just beneath the endothelium. As *Zygeupolia* has muscular crosses in its proboscis, the thin circular coat beneath the endothelium, described by Miss Thompson (30), might be comparable with these circular fibres.

Still another type of proboscis is found in the genera *Baseodiscus* (9) and *Joubinia* (9), at least in two of the three species belonging to this genus. The muscular coat consists again of two layers, one with longitudinal and the other with

circular fibres. Instead of the circular fibres lying beneath the epithelium as in Palæonemertines, the longitudinal muscles are found there (Text-fig. 14). The explanation would have been difficult, for either the layers might have been the inner longitudinal coat with a better-developed new circular layer as described in Lineids and Zygeupolia, or the outer

TEXT-FIG. 13.



Schema of the proboscis of Parapolia. *p.e.* Proboscis epithelium (outer surface). *o.l.m.* Outer longitudinal muscular layer. *o.c.m.* Outer circular ditto. *i.l.m.* Inner longitudinal ditto.

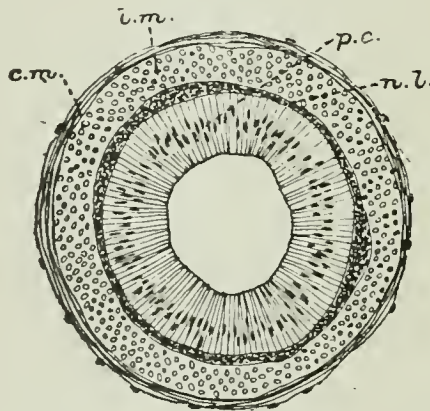
longitudinal and the outer circular muscle-layer, had not a form like *Joubinia rubens* Coe (11) or *Oxypolella* (3) existed. Both species show a different arrangement of the muscular fibres in the two parts of the proboscis (Text-fig. 15). The second part possesses the three muscle-layers characteristic of the body-wall of Heteronemertines. In the anterior part, however, the inner longitudinal fibres are absent, the wall showing the Baseodiscus type. The process of disappear-

ance of these longitudinal fibres, actually seen in *Joubinia rubens*, culminates in their total absence in *J. longirostris* and *blanca* and in *Baseodiscus*.¹ So if the Palæotype constitutes the first stage in its development, the three-layered muscular coat of *Cerebratulus marginatus* gives the second stage, *Baseodiscus* the third.

Putting all genera of Heteronemertines whose proboscis structure is known together in one list, we may find the links between the three above described stages.

Palæotype (Text-fig. 2): *Micrella rufa* Punnett, Oxy-

TEXT-FIG. 14.



Section through the introverted proboscis of *Baseodiscus* after Bürger (9, taf. 23, fig. 2). *p. e.* Proboscis epithelium. *n. l.* Nervous layer. *c. m.* Circular musculature. *l. m.* Longitudinal musculature.

polia beaumontiana Punnett, Euborlasia, *Cerebratulus urticans* (J. Müller) and other *Cerebratulus* species, Lineus

¹ Bergendal (4) described a *Valencinia longirostris* in which the so-called circular layer shows an interlacing of longitudinal and circular fibres something like the proboscis sheath of *Drepanophoridae*. The principal difference between Bergendal and Bürger (9), who gave this peculiarity of the proboscis of *Valencinia longirostris* in his figure, loc. cit., taf. 23, fig. 9, comes to this: that the circular fibres, according to the first-named author, are arranged in two planes, neither coinciding with the horizontal section of the organ, and that Bürger had not observed this fact. This, however, seems not to be of any importance to our conclusions, since both writers agree as to the circular nature of this musculature. The interlacing of fibres is, as has often been stated

bilineatus McIntosh, and other *Lineus* species, *Micrura atra* Punnett and other species; variations on this type, *Paralineus* (29) and *Zygeupolia* (Text-fig. 12).

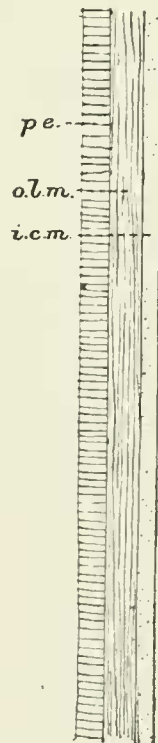
Transition to Heterotype: *Parapolia* (Text-fig. 13).

Heterotype (Text-fig. 16): *Cerebratulus marginatus* Renier, and other species, *Lineus versicolor* Bürger and

TEXT-FIG. 15.



TEXT-FIG. 16.



TEXT-FIG. 15.—Schema of the proboscis of *Joubinia rubens*.

Letters as in Text-fig. 13.

TEXT-FIG. 16.—Schema of the proboscis of *Joubinia longirostris* and *Basiodiscus*. Letters as in Text-fig. 13.

related species, *Micrura fasciolata* Ehrenberg Langia; variety *Joubinia longirostris* Berg.

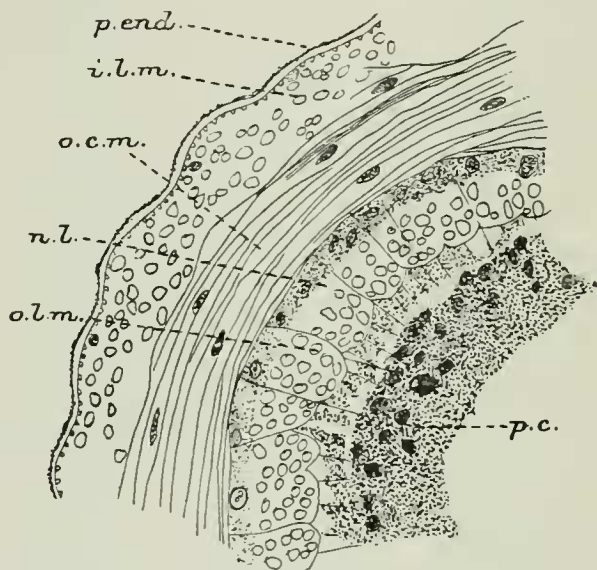
by other investigators, the result of the dissolving of muscular crosses, and seems therefore not to be of any consequence to our explanation. More compromising is the fact that in *Basiodiscus* the nervous layer, which I have not taken into consideration in this article, but which gives only support to my views, does not lie in the expected place between longitudinal and muscular fibres, but beneath the epithelium, as in *Palæonemertines*. Is this a reminiscence of a more primitive state?

Transition to Baseodiscus type: *Oxypolella* and *Joubinia rubens* (Text-fig. 15).

Baseodiscus type (Text-figs. 14 and 16): Baseodiscus species, *Joubinia longirostris* and *blanca* Bürger.

Two genera of Heteronemerteans, *Poliopsis* and *Valencinura* have not been mentioned yet. As regards *Poliopsis* this is due to our ignorance about its proboscis; in all the specimens which I know, it has been thrown off before capture. As

TEXT-FIG. 17.



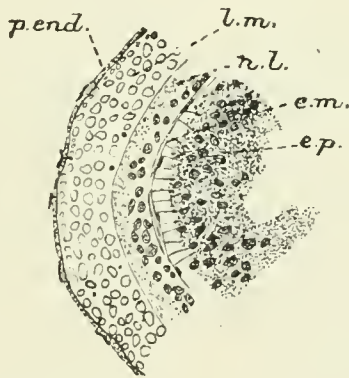
Section through the introverted proboscis of *Valencinura bahusiensis* after Bergendal (4. taf. 1, fig. 15). *p. end.* Proboscis endothelium. *p. c.* Proboscis epithelium. *n. l.* Nerve layer. Other letters as in Text-fig. 13.

regards *Valencinura* its proboscis has been described accurately by Bergendal (4). The anterior two parts of this organ possess a muscular coat very much like the anterior part of *Parapolia*'s proboscis. The third part, however, lacks all circular musculature. From the description given by Bergendal I cannot possibly make out whether the longitudinal fibres of this last part are the continuation of the outer or of the inner longitudinal layer. Two figures are given of the region in which the circular musculature is getting thinner before it disappears.

The order in which different coats are arranged is: Epi-

thelium, outer longitudinal layer, nervous layer, circular muscles, inner longitudinal muscle layer and endothelium with endothelial circular fibres (Text-fig. 17). The next section that is figured, however, gives: Epithelium, circular fibres, nervous layer, longitudinal muscle layer and endothelial circular fibres (Text-fig. 18). Probably, therefore, both outer circular and outer longitudinal muscle-fibres have disappeared, or, as in *Parapolia*, the outer longitudinal muscle-fibres have not yet been developed in the hinder part of the proboscis, and the outer circular muscular layer has disappeared, as it does in

TEXT-FIG. 18.



Section through the proboscis of *Valencinura bahusiensis* after Bergendal (4, taf. 1, fig. 14). *e.m.* Outer longitudinal muscles. *e.p.* Proboscis epithelium. Other letters as in Text-fig. 17.

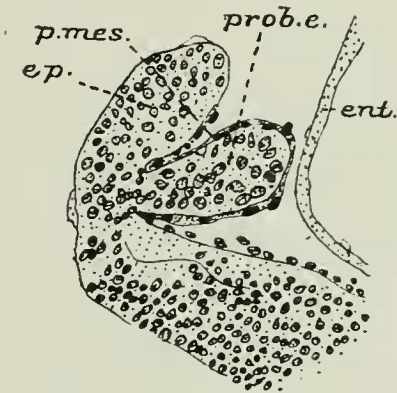
the other Nemertines. The place of *Valencinura* in our list should then be next to *Parapolia*; the nervous layer in changing places with the circular muscle-fibres, however, makes one cautious as to this supposition.

The facts taught by comparative anatomy, therefore, lead us to the conclusion that the proboscis of the Anopla is a structure of the body-wall in which both epithelium and muscular coat have taken part. We shall now have to consider whether all muscle-layers or only part of them helped to form the proboscis.

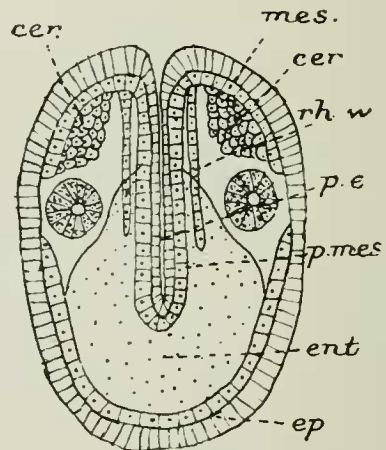
The body-wall of Anopla is, as Miss Thompson (30) tried to make certain, composed of four different muscle-layers. Of these all Palæonemerteans, with the exception of *Carinoma*,

only possess three, namely, the outer circular, the inner longitudinal and the inner circular muscle coat. In Heteronemerteans, as in *Carinoma*, an outer longitudinal layer of fibres has been developed. In the proboscides of Palæonemerteans we have found traces of no more than two of the three layers of the body-wall. Of the third or inner circular muscle-layer I have not been able to detect any traces in the proboscis of any Heteronemertean either, endothelial circular muscle-fibres being of an entirely different nature. Here embryology comes in to tell us where to look for the missing part.

TEXT-FIG. 19.



TEXT-FIG. 20.



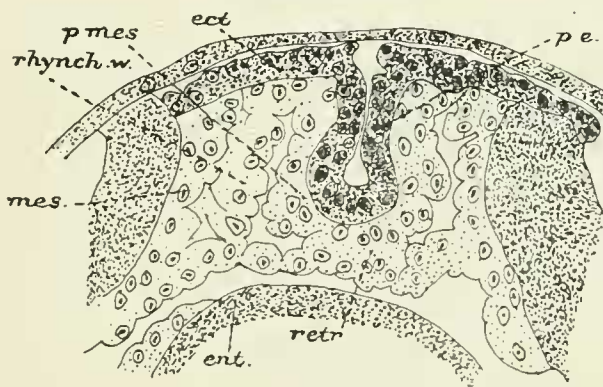
TEXT-FIG. 19.—Longitudinal section through an embryo of *Prosorochmus* after Salensky (28, taf. 3, fig. 27 A). *p.mes.* Proboscidian mesoblast. *ent.* Entoblast. *prob.e.* Proboscidian ectoblast. *ep.* Epiblast.

TEXT-FIG. 20.—Schema of an embryo of *Lineus obscurus* after Hubrecht (15, fig. 101). *rh.w.* Rhynchocœlomic wall. *mes.* Mesoderm. *cer.* Cerebral ganglia. *p.e.* Proboscis epithelium. Other letters as in Text-fig. 19.

A description of the development of the proboscis and its sheath is given by Salensky (25, 26, 27, 28), by Hubrecht (15), Bürger (7), Lebedinsky (18, 19, 20), and Arnold (1). Of these authors, Hubrecht, Bürger and Arnold studied the embryology of *Lineus ruber*, Salensky (26, 28) *Pilidium gyrans* (probably the larva of *Cerebratulus marginatus*) and *Pilidium pyramidale*. The Hoplonemertea subject to these investigations were *Prosorochmus viviparus* (Salensky,

25, 27), *Prostoma vermiculum* (Lebedinsky, 19, 20), and *Drephanophorus spectabilis* (Lebedinsky, 18, 20). All these investigations are essentially in agreement with each other as regards our subject, with the exception of Hubrecht's. This author, like the others, described the origin of the proboscis as an invagination of the ectoderm lying between, or, according to other authors, being part of, the two ectoblastic discs which give rise to the epidermis of the adult worm. All authors agree also as to the fact that this ectoblastic invagination, never becoming separated from the epiblast,

TEXT-FIG. 21.

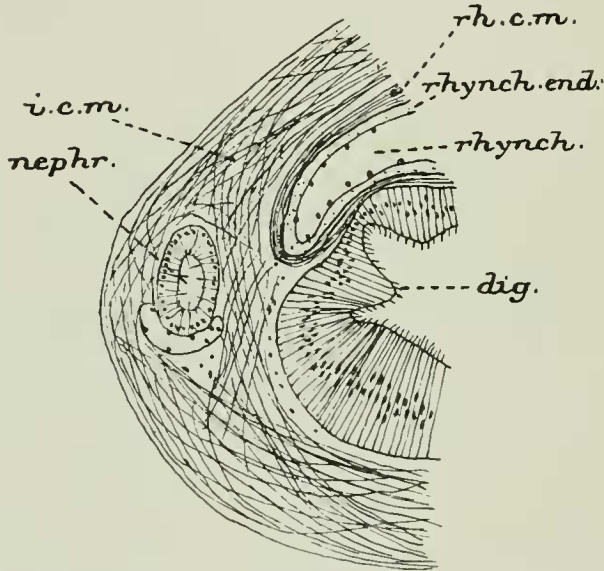


Section through the proboscidian system of an embryo of *Lineus* after Arnold (1, taf. i, fig. 18). *retr.* Retractor muscle. *ect.* Ectoblast. *ent.* Entoblast. Other letters as in Text-fig. 20.

gets its own mesoblastic investment, which is ectodermic in its origin (Text-fig. 19). At a later stage the ectodermic invagination of the proboscis has got two mesoblast layers separated from one another by a space. Hubrecht (15) considered that this second layer had grown out from the mesoblastic layer of the body-wall, cutting off part of the body-cavity, or, according to Hubrecht, part of the archocoel (Text-fig. 20). Later investigations, however, have shown that Hubrecht made a mistake. Bürger (7) studied Hubrecht's sections, and came to conclusions in perfect accordance with those of Salensky and all later investigators. The second mesoblastic layer takes its origin from the first one by delamination. Lebedinsky has described the presence of two "urmesoblasts" at the hinder

border of both layers. Two mesoblastic sacs take in this way the ectoblastic proboscis between them; when these sacs reach each other behind the proboscis, the retractor muscle is formed at the place where the walls fuse (Text-fig. 21). The inner layer gives rise to the muscular layers of the proboscis-wall; the outer to the wall of the sheath. Originally, however, these two structures belong together, their separation being brought about by a splitting of the mesoblast.

TEXT-FIG. 22.

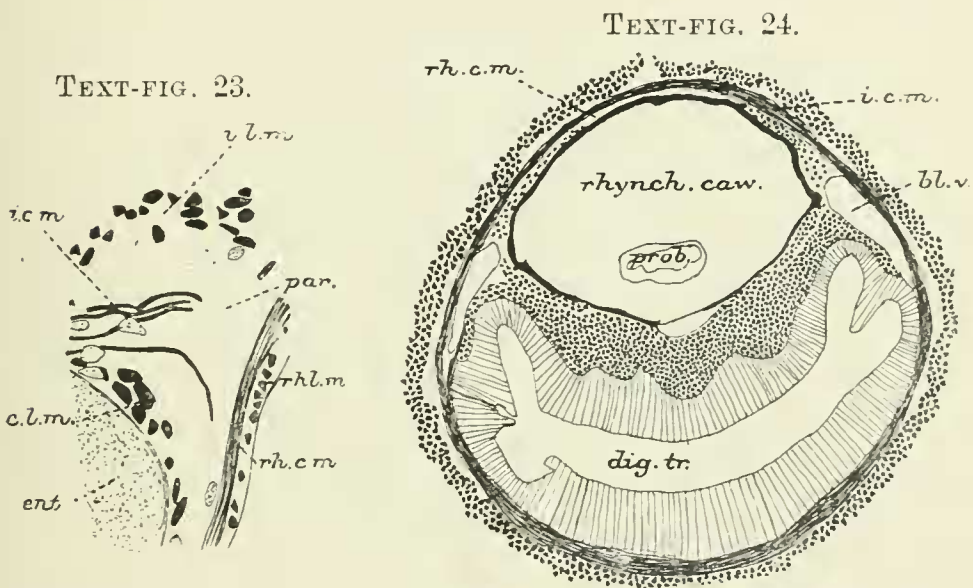


Section through *Carinina grata* after Bürger (9, pl. xi, fig. 3). *rhynch.* Rhynchocœlomic cavity. *rh.c.m.* Rhynchocœlomic circular musculature. *rhynch.end.* Endothelium of the rhynchocœl. *dig.* Epithelium of the digestive cavity. *i.c.m.* Inner circular muscle layer. *neph.* Nephridium.

Here we have found the evidence we looked for on p. 4. The proboscis has revealed itself as a part of the body-wall, of which the innermost layer of the muscular coat, the inner circular musculature, is absent. Embryology teaches that the proboscis sheath belongs to the proboscis, as both take their origin from the same tissue. We must, therefore, look for the missing part in the rhynchocœlomic wall. If the splitting took place between longitudinal and inner circular muscle-layer, the sheath must consist of a circular layer alone; if the longitudinal layer was the seat of these changes,

the wall of the rhynchocœlom should have an inner longitudinal and an outer circular muscular coat. The following facts anatomy discloses:

Procarinina possesses a proboscis-sheath, consisting of nothing but a very thin layer of circular fibres (5); in Carinina nothing but circular fibres are found (Text-fig. 22). Tubulanus linearis has a rhynchocœlomic wall, as Procarinina (9); in Tubulanus polymorphus inside this layer



TEXT-FIG. 23.—Part of a section through *Procephalothrix linearis*. *rh.c.m.* Rhynchocœlomic circular musculature. *rh.l.m.* Rhynchocœlomic longitudinal musculature. *c.l.m.* Central long. musculature. *i.l.m.* Inner, and *c.l.m.* central longitudinal muscles. *par.* Parenchyma. *ent.* Entoblast.

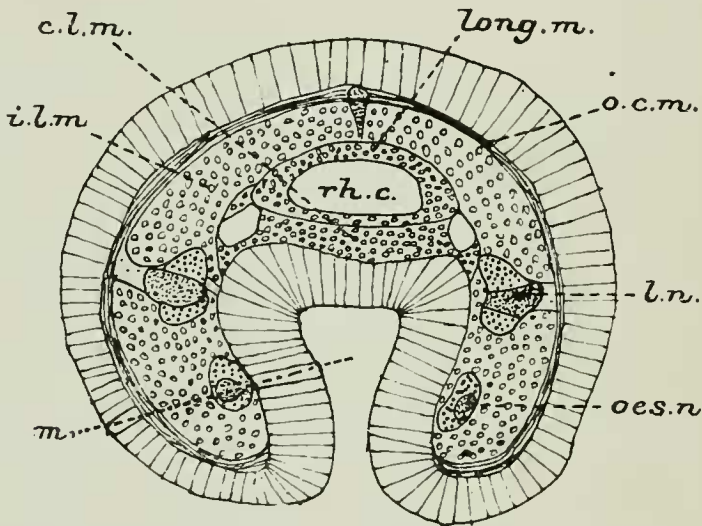
TEXT-FIG. 24.—Section through *Carinesta anglica*. *rhynch. cav.* Rhynchocœlic cavity. *rh.c.m.* Rhynchocœlomic musculature. *i.c.m.* Inner circular muscles. *prob.* Proboscis. *bl.v.* Blood-vessels. *dig. tr.* Digestive tract.

one row of minute longitudinal muscle-fibres can be found. Cephalotrichidæ (Text-fig. 23) agree with *Tubulanus polymorphus*, and so does *Hubrechtia*; but the *Callineridæ* (2) do not possess any longitudinal muscle-fibres inside the circular layer of the proboscis-sheath (Text-fig. 24).

The body parenchyma, in which the proboscidian system is imbedded, develops, as a rule, longitudinal fibres in the

Palæonemerteans. A localisation of these fibres is known to develop in several cases as the longitudinal septum between sheath and intestine, but also, as I have tried to demonstrate (31), as a longitudinal muscle-layer around intestine and proboscis-sheath, or as longitudinal muscle-bundles around the latter. In Procarinina these fibres have no connection at all with the sheath; neither have they in Carinina, in which a septum has developed. They seem to fail in Hubrechtia,

TEXT-FIG. 25.



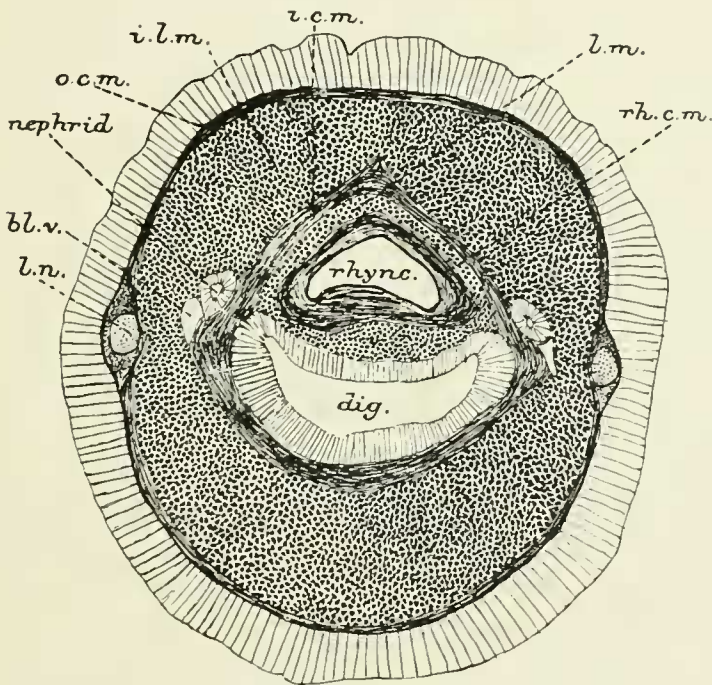
Section through *Cephalotrichella* after Bürger (9, taf. 11, fig. 14). *rh.c.* Rhynchocœlomic cavity. *long.m.* Outer rhynchocœlomic longitudinal musculature. *l.n.* Lateral nerves. *oes.n.* Oesophageal nerves. *m.* Mouth.

but are present in Carinina in the septum, as in some Cephalotrichidæ. In Callinera and some Tubulanidæ longitudinal fibres are present between the inner circular muscle coat of the body-wall and the rhynchocœlom, without building a distinct layer, as is the case in *Cephalotrichella signata* (Text-fig. 25), *Carinomella* (Text-fig. 9), and *Carinesta* (Text-fig. 26).

In all these cases they are regarded as being a new acquisition of the proboscis-sheath, developed out of the central longitudinal musculature. A strong support to this opinion is given in the behaviour of this musculature in the

family Cephalotrichidæ (31). Even different species of one genus as the two so nearly related species, *Procephalothrix filiformis* and *P. aliena*, show the development of a longitudinal musculature in the first and an ordinary septum in the other (31, 33). The Tubulanidæ show the same differences in one genus.

TEXT-FIG. 26.



Section through *Carinesta anglica*. *rhync.* Rhynchodæum. *rh. c. m.* Circular muscles of same. *l. m.* Longitudinal muscles of same. *dig.* Digestive canal. *nephrid.* Nephridium. *o. c. m.* Outer circular muscular layer of body. *i. c. m.* Inner ditto. *i. l. m.* Inner longitudinal ditto. *bl. v.* Blood-vessel. *l. n.* Lateral nerve.

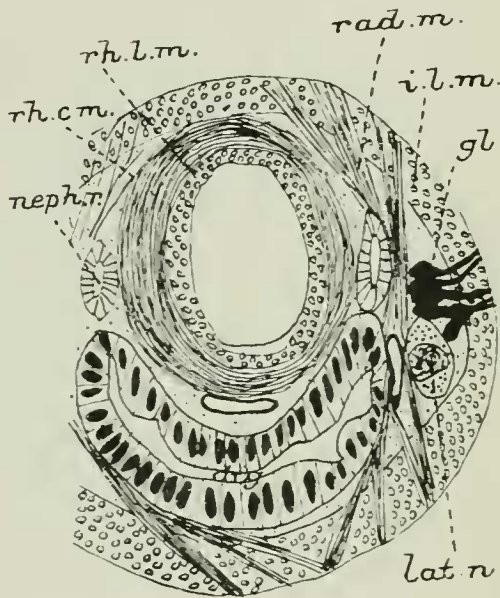
Therefore, if a longitudinal muscle-layer is developed outside the circular musculature of the proboscis-sheath, we must regard it as a secondary one, that has not been present *ab initio*, and not as an inherent part of this organ.

In *Heteronemertini* the two layers are noted. The circular muscle-layer is always present, an inner longitudinal coat has been recorded for *Euborlasia*, several *Linens* and *Cerebratulus*

species, *Joubinia longirostris*, *Micrura* and *Langia*, *Valencinura*, *Parapolia*, *Zygenpolia*, etc.

A secondary longitudinal muscle-layer does not seem to be frequent; as far as I know it is not present in any Heteronemertean. Therefore we may conclude that as a rule the proboscidian sheath of the Nemertea anopla consists of two layers, an inner longitudinal layer, which may be absent

TEXT-FIG. 27.

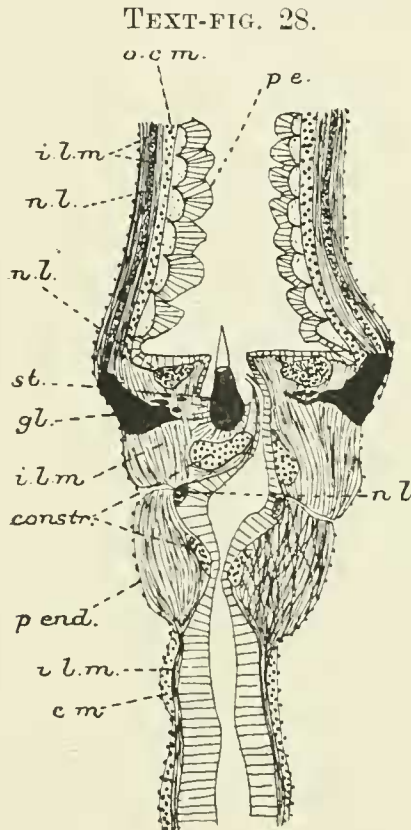


Section through *Emplectonema gracile* after Bürger (9. pl. xv. fig. 27). *rad. m.* Dorso-ventral musculature. *gl.* Glands. Other letters as in other figures.

(as in some Palæonemerteaus), and has sometimes the thickness of one layer of fibres, and an outer circular muscle-coat.

If ever theory were in accordance with the facts it is in this case. We were led to suppose that the proboscis was an inverted part of the body-wall by anatomical facts. One layer, however, failed, and embryology taught us that we might find it in the proboscis sheath, the two structures belonging together and being one in ontogeny. The missing part is, as a matter of fact, found in the proboscis sheath, and this consists of the two layers we knew a priori it must consist of, if the supposition were right. We conclude,

therefore, that in Nemertea anopla the proboscis and its sheath have phylogenetically the same origin, both being part of an inverted portion of the body-wall; that the two structures became separated by a rent in the muscular coat, which took place in the inner longitudinal or between the two inner muscle-layers. The proboscis has, at least, three layers,



Longitudinal section through the proboscis of *Prosorochmus* after Bürger (9, pl. xxiii, fig. 14). *st.* Stylet. *gl.* Glands. *constr.* Constrictor. *c.m.* Circular muscle layer. Other letters as in previous figures.

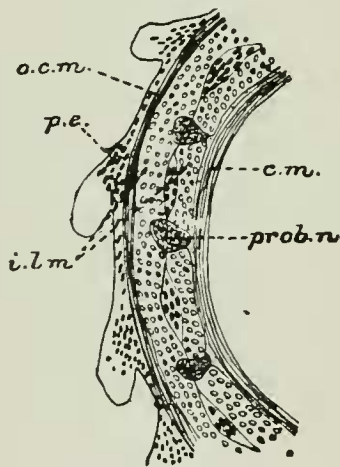
if reduction does not take place: the epithelium, the outer circular and the inner longitudinal muscle-layer, an outer longitudinal layer not necessarily developing, if it is present in the body-wall. The proboscis sheath has two or one muscular coat, an inner longitudinal layer, if present, part of the inner layer of the body-wall, and an outer circular muscle layer, the inner circular muscle-coat of the body-wall.

I have purposely not confused these facts and conclusions in Anopla with those in armed Nemerteans, for the development of the armature in Hoplonemertea has so specialised this organ, that we must expect great deviations from the original conditions.

The genus *Malacobdella* also lives under such unnatural circumstances for a Nemertine that all kinds of anomalies may be expected.

Of the three original muscle-layers of the body-wall, the

TEXT-FIG. 29.



Section through the proboscis of *Amphiporus pulcher* after Bürger (9, taf. 23, fig. 3). Letters as in other figures.

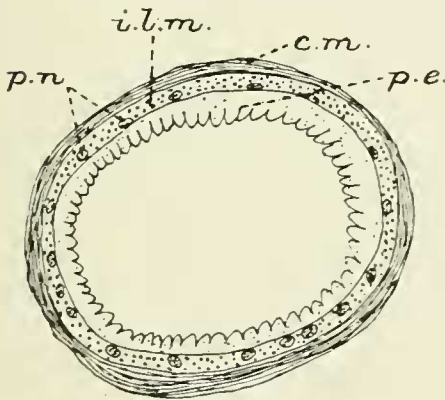
inner circular fibres, as such, are never present; we have to look for them, as has been demonstrated by Miss Thompson (30), in the dorso-ventral musculature of the body (Text-fig. 27). The outer longitudinal muscle-layer of Heteronemertini has nowhere developed, and we can recognise the other longitudinal layer by the nervous system being imbedded in it. Therefore we shall have to look for three muscular layers in the proboscidian system: a circular and a longitudinal layer, the latter possibly giving notice of its nature by the seat of the nerves, both in the proboscis, and probably remnants of the same longitudinal layer, and a circular layer in the wall of the sheath.

Now let us examine the facts. *Malacobdella* has a proboscis

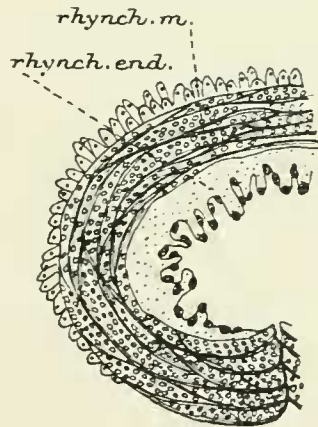
as described above, an epithelium with a circular muscle-layer underneath, and the longitudinal layer divided into two parts by a nervous layer. The endothelium, which lines both proboscis and sheath, is in the latter structure followed by a circular muscle-layer, as the presence of longitudinal muscle-fibres between them seems to be doubtful (9). These facts are in perfect accordance with those in *Anopla*.

In *Hoplonemertea* some diversity exists as to the structure of the sheath. In all species, however, the wall of the proboscis has developed in a very similar way. As a rule we can

TEXT-FIG. 30.



TEXT-FIG. 31.



TEXT-FIG. 30.—Section through the hinder part of the proboscis of *Amphiporus marmoratus* after Bürger (9, pl. xxiii, fig. 18). *p. n.* Proboscis nerves. Other letters as in previous figures.

TEXT-FIG. 31.—Section through the rhynchocœlomic wall of *Drepanophorus* after Bürger (9, taf. 23, fig. 37). Letters as before.

divide the proboscis into three parts (Text-fig. 28), the middle part being the seat of the characteristic structures. Of these parts the first region has a wall consisting of three muscle-layers, two of which are circular coats separated by the only longitudinal coat in which the nervous layer is present (Text-fig. 29). The longitudinal coat, therefore, must be regarded as the inner longitudinal layer of the body-wall, and naturally one looks upon the circular layer between epithelium and longitudinal fibres as the outer circular muscle-coat. The other circular layer is present throughout the whole length

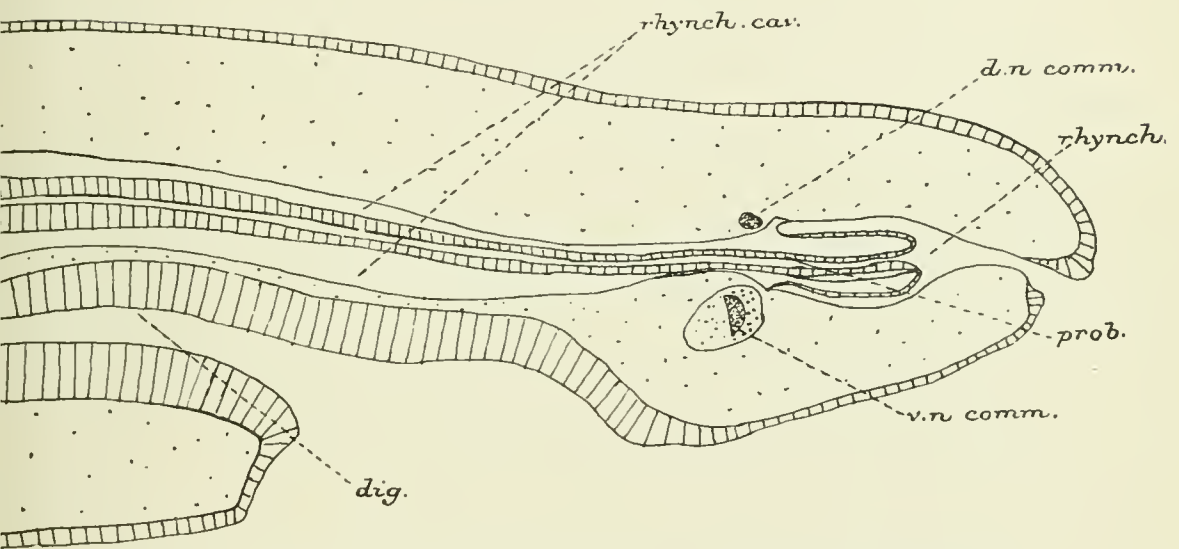
of the proboscis, as is the longitudinal layer. The outer circular muscle-layer, however, has absolutely disappeared in the hind part of the proboscis (Text-fig. 30), and is found in the middle part in the shape of two distinct sphincters (Text-fig. 28). One might feel inclined to regard the second circular layer as the inner circular coat of the body. This, however, is not in accordance with the embryological facts, that taught us to regard the sheath as part of the body-wall. Moreover, this sheath has a musculature exactly like that of *Anopla*. In all *Hoplonemertea* two muscular layers are present—an inner longitudinal layer often feebly developed, and an outer circular layer (Text-fig. 29). There is no reason not to regard them as identical with the same layers in *Anopla*, and therefore the inner circular muscle-coat of the body-wall is represented by this circular layer of the sheath, the longitudinal fibres being part of the inner longitudinal musculature. The family *Drepanohporidæ*, however, has a differently constructed sheath, in which, as in the hinder part of the same structure in *Carinoma*, longitudinal and circular fibres have become interlaced (Text-fig. 31).

We have already discussed a similar process in connection with the proboscis of *Joubinia longirostris*. As two kinds of fibres are present, and in all related genera these fibres are situated in the way stated above, we might regard their arrangement in *Drepanophorus* as a complication of that stage, which cannot disturb our view of the facts.

So homologues of all layers of the body-wall are found in *Hoplonemertea* in exactly the same place as in *Bdellonemertea* and in *Anopla*; the second circular layer of the proboscis, however, cannot be homologised with any part of it, neither do we know any such layer in *Anopla*. However, two cases are known, in which a tendency seems to exist to form a new circular layer underneath the endothelium; Bergendal (6) described the presence of circular fibres at that position, caused by the existence of faint muscle crosses (Text-fig. 3). C. B. Thompson (30) showed the presence of a layer of endothelial muscle-fibres. Though both are probably of a

totally different nature, we may look for an analogy between the development of this second circular muscle-layer in the proboscis of *Hoplonemertea* and the above described structures. Moreover, the *Hoplonemertea* have such a highly developed proboscis with a stylet, reserve stylets, the presence of the whole middle part (Text-fig. 28) with its glands and ejaculatory duct, etc., that the obtaining of a new muscle-layer seems nothing compared with the development of the

TEXT-FIG. 32.



Schema of a longitudinal section through *Cerebratulus marginatus* after Bürger (9, pl. xxi. fig. 1). *d.n. comm.* Dorsal nerve commissure. *v.n. comm.* Ventral nerve commissure. *rhynch.* Rhynchodæmu. *dig.* Digestive tract. *prob.* Proboscis. *rhynch. cav.* Cavity of the rhynchocoel.

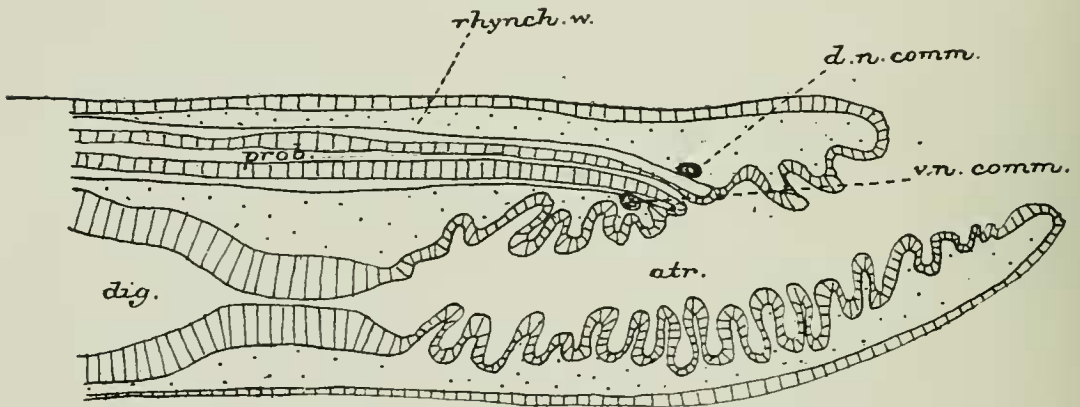
armature. And if we regard this layer as an acquisition of the proboscis itself, the facts found in *Enopla* are in perfect accordance with those in *Anopla*.

After all, it seems to me that the structure of the proboscis in all Nemertean together with the structure of the rhynchocoelom can only lead to this conclusion, that they both took their origin from the body-wall, a separation being brought about in the musculature, which, as in embryology, caused the development of a proboscis and of a sheath.

Proboscides have been described in many invertebrates;

they are known in Cestodes, in Turbellaria, in Hirudinea, in Acanthocephala, in Sipunculids and Priapulids, in Echiurids and in Kinorhyncha, and in Nemertines. There can be no doubt that these proboscides are not homologous with one another. In Kinorhyncha, Priapulids and Sipunculids the so-called proboscis consists of the anterior part of the body, bearing the mouth at its top. The body-cavity extends into this part, and muscles extend from this region of the body-wall to the wall of the trunk, causing the invagination of the anterior part as a prolongation of the pharynx.

TEXT-FIG. 33.



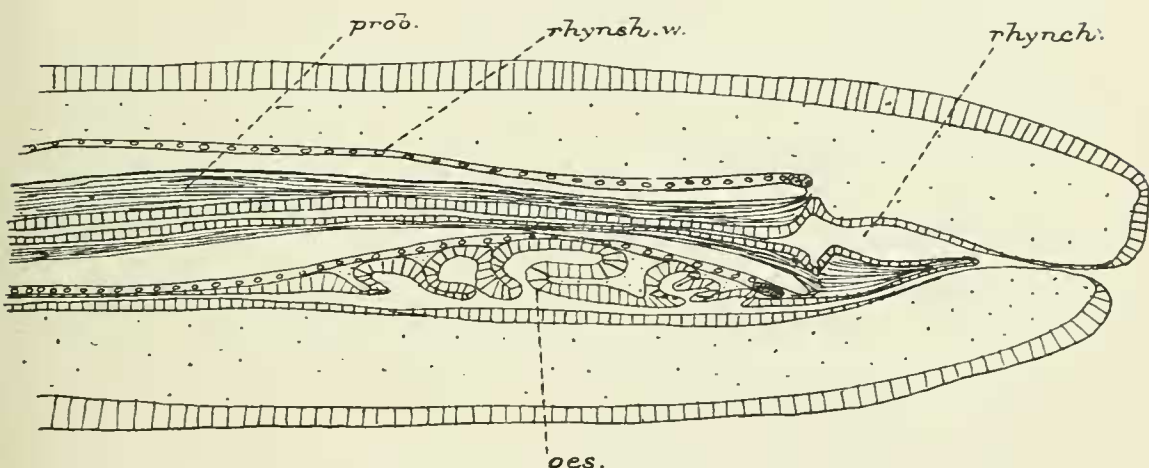
Schema of a longitudinal section through *Malacobdella grossa* after Bürger (9, pl. xviii. fig. 2). *atr.* Atrium. *rhynch. w.* Rhynchocœlomic wall. *d. n. comm.* Dorsal nerve commissure. *v. n. comm.* Ventral ditto. *dig.* Digestive tract.

In Hirudineæ the so-called proboscis is quite another structure. The wall of the pharynx of Rhynchobdellida shows a protrusible part, which bears the opening of the intestine at its extremity when erected, in the manner of the pharynx of Turbellaria. Now, Bürger (8) suggested that the pharynx of Turbellaria is homologous with the proboscidean system of Nemertea. Both structures, therefore, must be considered more closely in this connection.

Bürger was brought to this conclusion by certain very characteristic features in Enopla. For, though in all Anopla the proboscis is extruded through a separate proboscis-pore situated in front of the brain (Text-fig. 32), and the mouth is

always found behind the cephalic ganglia, digestive and proboscidean systems having no connection whatever with each other, they are closely connected in all Enopla (Text-figs. 33 and 34), with the exception of Drepanophoridae. The genus *Malacobdella*, in many features so widely different from all *Hoplonomertea*, shares this character, though the way in which digestive tract and proboscidian system are connected is quite exceptional in *Malacobdella* (Text-fig. 33). The mouth is situated at the anterior extremity of the head, being

TEXT-FIG. 34.



Schema of a longitudinal section through *Nemertopsis peronea* after Bürger (9. pl. xv. fig. 1). *rhynch.* Rhynchodæum. *rhynch. w.* Rhynchocœlomic wall. *prob.* Proboscis muscles. *oes.* œsophagus.

wide and slit-like as in many *Heteronemerteans*, and giving entrance to the large œsophagus which lies underneath the cerebral ganglia, and into which the intestine proper opens. The rhynchodæum, which, in fact, is so small that as such it does not seem to exist, opens into the dorsal wall of the œsophagus, the anterior part of the latter being called atrium because of this fact.

In *Hoplonomertea* exactly the reverse of this condition is found (Text-fig. 34); here the proboscis-pore opens to the exterior, giving entrance to a well-developed rhynchodæum, in the hinder part of which the proboscis is inserted. Through

an opening in the ventral wall of the rhynchodæum the œsophagus gets an open connection with the rhynchodæum. Bürger took the rhynchodæum to be the homologue of the atrium of *Malacobdella*, and declared the proboscidian system to be a kind of appendix of the digestive organs. As both œsophagus and rhynchodæum originate by invagination of the ectoblast, lined by the mesoblastic layer which gives rise to the muscular coat of these organs, Bürger's hypothesis seems to be not impossible.

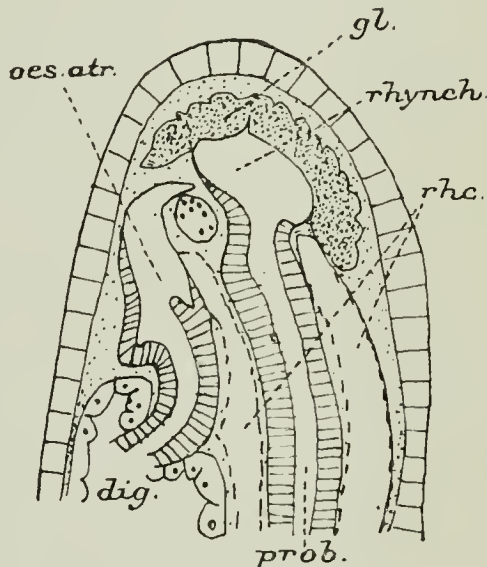
Bürger (8), who stands for the Turbellarian relationships of Nemertea, compared the intestine of both classes, and found a pharynx in the first and a proboscidian system in the other class without any homologues. He then suggested that they were themselves homologous, both being derived from the epiblast and the mesoblast underneath. The pharyngeal sac of *Turbellaria* should be the homologue of the atrium s. rhynchodæum in *Nemertea*. The great difference between the two organs, however, consists in their different relation to the œsophagus, which passes right through the pharynx, and has no direct connection with the proboscis; for Bürger suggested, as we have done, that a splitting must have taken place in the muscular coat of the pharynx, giving rise to a rhynchocœlom. This seems altogether very plausible, but how is the emancipation of the pharynx from the digestive tract to be explained? Bürger says: "Denken wir den Pharynx nicht in den Vorderdarm gestülpt, sondern über oder vor der Anlage des Vorderdarms in das Parenchym gewachsen und dann einen Spalt im Mesoderm des so verschobenen Pharynx entstanden, dieses in zwei Blätter teilend, so bekommen wir den Pharynx in einer vor oder über dem Vorderdarm befindlichen Höhle mit mesodermaler Wandung zu liegen, welche dem Rhynchocœlom homolog sein würde, der Pharynx selber aber verhielte sich vollständig wie der Nemertinenrüssel." The way in which the œsophagus must attain a direct communication with the pharyngeal sac is rather absurd: "Es ergibt sich ohne Weiteres, dass wir in dem Pharynx ein Zuviel haben, denn nur seine Tasche, die,

nachdem wir den Pharynx exstirpiert haben, direct mit dem Darm communiciert, entspricht dem Nemertinen vorderdarm." Even if Bürger did not suppose this mode of arriving at the described situation to have really taken place, as I am sure he never did, I cannot see in what other way the pharynx could be emancipated from the digestive tract. It is quite impossible to picture the way in which these changes had to take place without any such lesion, and on this ground alone the theory of Bürger seems to lose vitality. But there is more. Bürger gives three reasons to support his views. The first one we have already given above. The second support is found in embryology: "Der Nemertinenrüssel entsteht stets aus einer Ectodermeinstülpung, die mit einem diese umgebenden Mesodermwulste verschmilzt. Die Anlage des Rüssels erfolgt bei den Metanemertinen am selben Orte wie die des Vorderdarms und mit ihr gemeinschaftlich." The similarity of histological structure of the two parts is the third one. As to the latter, the histological resemblance of pharynx and proboscis consists only in the presence of an epithelium and the muscular layers of the body-wall, and therefore the same statement as before, that both are structures of the body-wall, must be repeated. Real histological resemblance there cannot possibly be, as the epithelium of the proboscis in Nemertines shows a great variety of elements in different parts and different species. That the muscular tissue of Nemertines and Turbellaria agree in structure is too well known to have any proving importance in this case, for the proboscis musculature is built up in exactly the same way as the muscles of the body-wall. Bürger's third reason, therefore, is not at all convincing. The embryological facts, which follow in the second place, have since been contradicted by Lebedinsky and Salensky. In the first place, Bürger compares the invagination of the proboscis-ectoderm with the extirpation of the pharynx-ectoderm; then the pharyngeal sac is the primarily planned organ, the pharynx developing afterwards at the bottom. In Nemertines the proboscis is the organ that appears first,

a later invagination of ectoderm giving rise to the rhynchodæum, the homologue of the pharyngeal sac.

But even if one takes into consideration the plain embryological facts in Nemertines, it seems difficult to come to the same conclusions as Bürger. For in what way do Nemerteans get a mouth? In Anopla the blastopore sometimes, after becoming closed, is transferred to the inside of the animal by the invagination of the œsophagus. In Enopla the facts are

TEXT-FIG. 35.



Longitudinal section through *Prosorochmus* after Salensky (27, fig. 8). *oes. atr.* Œsophageal atrium. *rhynch.* Rhynchodæum. *rh. c.* Rhynchocœlomic cavity. *gl.* Glands. *dig.* Digestive canal. *prob.* Cavity of inverted proboscis. *rhc.* Rhyncocæl.

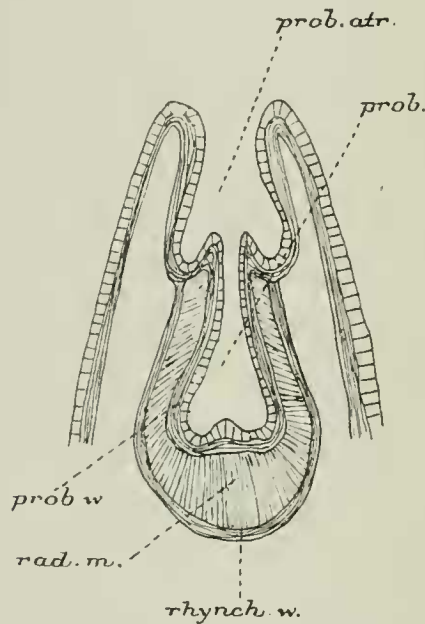
less simple. *Drepanophorus*, the genus in which œsophagus and rhynchodæum open separately, shows no connection at all between the two systems, not even in embryology; for here the blastopore is closed, the narrow entodermic part giving rise to the blind gut by being removed forward. The primary ectodermic œsophagus invaginates near the proboscidian system, but perfectly separate. The place where œsophagus and entoderm communicate in *Drepanophorus* has, therefore, nothing to do with the same spot in *Hetero-*

nemerteans. In all other *Hoploneurtea* the primary œsophagus originates in exactly the same way; the mouth closes afterwards, and the primary œsophagus gets a new opening to the exterior through the rhynchodæum. Lebedinsky described in *Tetrastemma vermiculus* how the rhynchodæal epithelium grows towards the œsophagus, a bifurcation of the cavity being produced. Salensky (27), however, is of opinion that in *Prosorochmus* the communication is brought about by the œsophagus, which has produced through histological differentiation an atrium of its own (Text-fig. 35). The difference of opinion between these two authors does not matter in the least for our decision, for it is evident that the conditions in *Drepanophorus* are primitive, and that the facts on which Bürger based his theory are not primitive at all, as the *Drepanophorus* stage is passed through in ontogeny. This fact, the difference between the communication in *Malacobdella* and *Hoploneurtea*, the impossibility of a pharynx developing into a proboscis, the difference of origin between the two organs, the differences in the connection between pharyngeal sac and pharynx at one side, proboscis and rhynchodæum at the other, the insufficiency of the grounds on which Bürger bases his theory, make me very sceptical as to its value. In fact, I cannot find any other point of resemblance between the two organs than that they are derivatives of what the Germans call *die Hautmuskelschlauch*.

There are, however, other organs in Invertebrates, even in *Platyhelminthes*, which have a similar origin, and we shall have to look for comparison between them. For example, the proboscis of *Echiurids* is a structure of the body-wall—at least it consists of an epidermis and muscles only; moreover it is situated in front of the mouth, and is known to be very elastic. As, however, this proboscis is supposed to be the præoral lobe of the larva and cannot be retracted into the body, it does not give any special indication of affinity to the same structure in Nemerteans. In *Acanthocephala* (14) a proboscis is found, which can only partly be retracted into the body. The proximal part is surrounded by a sheath of

muscles, the circular fibres of which act as protractors; the retractor muscle, which retracts proboscis and sheath, the two parts being continuous, is inserted at the hind end of the sheath, and extends through the body-cavity to the body-wall. Though some agreement in these structures in Echinorhynchus and Nemertea cannot be denied, I do not suppose there is any relationship between them. The proboscidian system of Acanthocephali is entodermic in origin and only secon-

TEXT-FIG. 36.



Schema of the proboscis of *Macrorhynchus croceus* after von Graff (13, pl. x, fig. 12). *prob. atr.* Proboscidian atrium. *prob.* Cavity of the introverted proboscis. *prob. w.* Proboscidian wall. *rad. m.* Radial musculature. *rhynch. w.* Rhynchocoelomic wall (Muskelzapfen). Compare with Text-fig. 1.

darily gets its epidermis. This fact alone seems to exclude all possibility of homology with the proboscis of Nemerteans.

Coming to the consideration of two other structures, both in Platyhelminthes, the proboscides of Tetrarhynchus and of Proboscida, the four proboscides of the characteristic genera of Cestodes superficially show a great resemblance to those of Nemerteans. The proboscis is an introvert,

being retracted by a muscle-bundle at the bottom of the tube just as in Nemertines. A muscular sheath is present, separated from the proboscis by a cavity filled with a liquid. Histologically, however, a great difference seems to exist. For instance, the proboscis itself has no muscles at all, if I understand Pintner (21) right; the wall of the sheath is differently constructed at its anterior and posterior part, a muscular sheath only existing in the hinder part, the anterior being a derivative of the ectoderm. Moreover the proboscides of these Cestods are paired, those of Nemertines being unpaired.

Much more striking is the likeness to the proboscis of *Turbellaria proboscida*. Salensky (25 and 26) was the first to compare them, and though he already proclaimed them homologues in 1884, nobody seemed to agree with his opinion. Hubrecht (16) raged against it, and afterwards Bürger (8) gave a new theory. Salensky, however, was not convinced, and tried to give fresh support to his hypothesis in his articles of 1909 and 1912 (27, 28).

The proboscis, which is found in certain genera of Rhabdocoelida, is localised at the anterior end of the head. Von Graff (13) described the organ in this way: "Der Proboscidenrüssel ist nichts weiter als eine bleibend gewordene Einstülpung des Vorderendes, wie wir sie vorübergehend bei *Mesostomum rostratum* entstehen sehen." It consists of two parts, the proboscis and a kind of atrium, through which the proboscis is everted (Text-fig. 36). The cavity of both is lined by the somewhat changed epiderm. The wall of the atrium has, like the body-wall, a muscular coat, which is the direct continuation of the muscular layers of the body-wall. At the base of this sac or atrium the proboscis is inserted. Here the muscular coat is broken up into two layers; the inner layer continues along the epidermis, the other one forms the outer lining of the proboscis. A thick layer of radially placed muscle-fibres fills the space between the two parts of the muscular coat of the body-wall. In Nemertines (Text-fig. 1) we find the same arrangement: an atrium to the proboscis, being part of the

body-wall, that has grown inward and is called rhynchodæum. The continuation of the epithelium is found in the epithelium of the proboscis. The muscular coat of the body-wall is split, and has given rise to the muscular wall of the proboscis and of the sheath. The cavity of the rhynchocœl is even traversed by a band of radially placed muscle-fibres, the retractor muscle. So Salensky (26) proposed the following homologies.

Rhabdocèles proboscifères.

Némertiens.

- | | |
|---|-------------------------------------|
| 1. Poche de la trompe. | 1. Vestibule de la trompe. |
| 2. Epithélium de la trompe. | 2. Epithélium de la trompe. |
| 3. Couche interne de la calotte musculaire (Muskelzapfen v. Graff). | 3. Couche musculaire de la trompe. |
| 4. Couche externe de la calotte musculaire. | 4. Parois de la gaine de la trompe. |
| 5. Muscles radiaires de la calotte. | 5. Bride musculaire. |

When von Graff (13) described the structure of the proboscis of *Macrorhynchus* and other Rhabdocœlida the origin of the proboscis and sheath in Nemertines was not known. He could not find any homologue of the sheath in his genera, and on this ground denied any relationship between the proboscides in these two classes of Platyhelminths. Another ground for denying it was found in the division of the proboscis of Nemertines into two parts, the posterior glandula part not being present in *Turbellaria proboscida*. This ground, however, seems not to be very important; the proboscis of Rhabdocœlida represents rather a simple stage of organisation in comparison with the same structure in Nemertines. It does not seem to be necessary to go into such details of structure, especially not since we know what a great variety of epithelial structure is to be found in different genera of Nemertea.

Salensky looked for support for this theory to embryology. And certainly the fact that the muscular coats of rhynchocœlomic and proboscidian walls take origin out of the same

layer of mesoblastic elements, a splitting giving rise to the cavity of the sheath, is highly in favour of his views. It was exactly on this point that Hubrecht did not agree with him; therefore Hubrecht, who, moreover, claimed the Annelida-relations of Nemertea, could not possibly follow Salensky. As, however, later investigations proved that Salensky was right, this reason for disagreeing with his theory gave way. But Hubrecht gave other reasons. In the ‘“Challenger” Report’ he wrote, p. 104: “Salensky would probably not have made his startling hypothesis above alluded to, based on ontogenetical observations of a scission in the proboscidian wall, by which (1) a muscular proboscidian sheath surrounding the proboscis becomes separated from, and independent of, the musculature of the proboscis itself, and (2) an isolated coelome—the proboscidian cavity—is originated, if he had been as well acquainted with the comparative anatomy of the animals about which he writes as he is with certain details of their ontogeny.” The anatomical facts, that tell against Salensky, Hubrecht summarises in this way (*loc. cit.*, p. 103): “There can hardly be any doubt, when we take into consideration all the morphological data at our disposal, that the muscles composing the proboscidian sheath gradually took their origin by the increase and modification of pre-existing muscular elements which belonged to the body-wall and to the body-parenchyma before the proboscis, modified from a tactile organ, as it appears to have primitively been, had yet become evolved, through the growth inwards of the anterior tip of the body, into an aggressive weapon with stylet or nematocysts, etc.” Since this was written many facts have been disclosed as to the anatomy of the proboscidian system, and we have seen that they lead us to the conclusion, that the sheath is part of the body-wall, and has not originated *in loco* out of muscular fibres in the parenchyma of the body. The central parenchyma does not possess any circular muscle-fibres. Wherever other than longitudinal fibres have been found in it they have been demonstrated to be part of one of the layers of the body-wall, as a rule the inner circular

muscle-layer. Longitudinal muscle-fibres may be present in the central connective tissue, and we have already seen that in some cases they are arranged around the proboscis sheath so as to form a secondary longitudinal coat. This, however, is not the rule, not even in *Anopla*, where a central longitudinal musculature is developed in the majority of genera. Our conclusion is exactly the reverse of the above statement of Hubrecht; the facts described in the first part of this article seem not to allow the denial of our conclusion. Both on anatomical and embryological grounds we must declare the muscular coats and walls of the proboscidian system of *Nemertines* to belong together *ab origine*; the facts put forward by Hubrecht against the theory of Salensky have been refuted by later embryological investigations. I hope to have given a new support to Salensky's ingenious theory by this comparative study of the anatomy of the proboscidian system. The fact, stated by Hubrecht, that "we find the shorter proboscides and the less significant proboscidian sheaths among the more primitive genera of *Nemertea*," is, though mentioned by him as telling against the *Turbellarian* relations, in perfect accordance with, if not in favour of, Salensky's theory.

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